PRELIMINARY ACCOUNT OF THE CELL LINEAGE OF PLANORBIS.

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THE eggs of Planorbis are deposited in capsules which are usually found fastened by a viscid secretion to stones or aquatic plants. In *P. trivolvis*, the species studied, the period during which eggs are laid extends from early spring until late in the fall. The eggs contain somewhat less than the usual amount of yolk; there is a clear, protoplasmic area at the animal pole, while the lower half of the egg is composed principally of deutoplasm.

In the matter of nomenclature I have followed Conklin in designating the different cell generations given off from the macromeres by coefficients instead of exponents. For instance, 1*a* would represent a cell of the first generation of ectomeres, 2*a* one of the second, and so on.

At the first cleavage the egg is divided into equal blastomeres, and the four-cell stage is produced by the almost simultaneous division of these two blastomeres into subequal cells. This division takes place in a right-handed spiral; two of the cells *B* and *D* meet in a cross furrow at the vegetative pole, while the other two blastomeres, *A* and *C*, come in contact above. The first cleavage furrow is oblique to the future longitudinal axis of the embryo; a plane cutting the centers of *B* and *D* nearly coincides with the future sagittal plane. A cleavage cavity makes its appearance in the two-cell stage, reaching its maximum size immediately before the division into four cells. Small cavities commonly occur between the blastomeres during several subsequent stages of cleavage.

The first quartette of ectomeres is given off in a left-handed spiral, the cells 1*a* and 1*c* meeting in a cross furrow at the apical pole. This division is followed by a dexiotropic cleavage of the macromeres, and soon afterward the first generation divides in a dexiotropic direction, thus giving rise to a

sixteen-cell stage. The lower tier of cells resulting from the latter division are the trochoblasts or turret cells of Conklin. A third quartette of ectomeres is given off in a left-handed spiral, completing the separation of the ectoderm; at the same time a laeotropic division occurs in the second quartette. The form of the egg which now contains twenty-four cells is almost spherical; there is a large cleavage cavity which is not, however, in any way homologous with that of the two-cell stage. The macromeres are much smaller than is usual among the eggs of the mollusca; in fact they scarcely exceed in size the

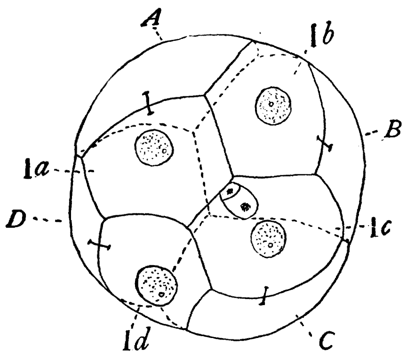

FIG. 1. — Egg of eight cells.

cells of the third quartette. They are quite conspicuous, however, on account of the yolk granules they contain which give them a bright golden yellow color.

The resting period which occurs at the twenty-four-cell stage is broken by the dexiotropic cleavage of the upper tier of the second generation of ectomeres ($2a^1$, $2b^1$, etc.); and, at nearly the same time, the posterior macromere *D*, by a dexiotropic division, gives off the cell *4d* which is destined to produce the mesoblastic bands. The ventral moiety of this division, compared with the mesoblast cell, is small, and, as far as it could be observed, remained undivided. The remaining macromeres do not divide until a somewhat later period. The ventral tier of the second quartette next divides dexiotropically; there are now four groups of four cells each belonging to the second generation of ectomeres, one cell in each group being above and one below, while there is a right and a left cell at the same level.

The divisions of the four cells of the third quartette and both tiers of the first quartette quickly follow. The pairs of cells belonging to the third quartette are arranged radially as in Limax (Kofoid), the one cell lying above the other. After these divisions the cross makes its appearance, becoming a very conspicuous feature of the egg. The cells of which it is composed are the eight cells resulting from the laeotropic division of the apical cells of the first generation of ectomeres and the four upper cells of the second quartette which form the tips of the arms. The angles between the arms of the

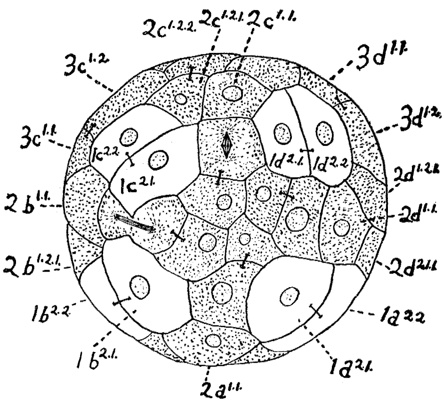

FIG. 2. — Egg of sixty-four cells, seen from above.

cross are occupied by the four pairs of trochoblasts ($1a^{2.1}$, $1a^{2.2}$, $1b^{2.1}$, $1b^{2.2}$, etc.). Compared with Crepidula (Conklin) and Umbrella (Heymons), in which the trochoblasts divide only at a very late period of cleavage, the division of these cells occurs remarkably early. In this respect Planorbis agrees much more closely with Limax (Kofoid), in which the corresponding cleavage occurs at near the forty-cell stage. Both in Crepidula and in Umbrella the trochoblasts are small, but in Planorbis they are conspicuous from their large size and transparency.

The next cells to undergo division are the three entomeres *A*, *B*, and *C*, the corresponding division of *D* having taken place at an earlier period. This cleavage is dexiotropic, the cells at the vegetative pole being much smaller than those of

the upper or fourth quartette. At about this time the large mesoblast cell *M* divides; the two resulting mesomeres lie partly pushed into the cleavage cavity so that only a small portion of each appears at the surface. They become entirely covered over by the ectoderm at about the sixty-four-cell stage. With the division of ectomeres and the mesomere the number of cells has reached forty-nine. This stage marks another resting period. The egg has now seven entomeres, two mesomeres, and forty ectomeres, the first and second generations of ectomeres each containing sixteen cells, while the third quartette is composed of eight. Up to this time all of the ectodermic cells of a quartette have undergone division at approximately the same time. The cleavage of certain cells of the third quartette which now takes place introduces an exception, in this respect, to the previous regularity of cleavage. The anterior cells of the lower tier of the third quartette, $3b^2$ and $3c^2$, divide bilaterally, and, at nearly the same time, the two posterior cells of the upper tier of the same quartette, $3a^1$ and $3d^1$, undergo a division which is likewise bilateral. The large cells $3a^2$ and $3d^2$ remain for a long time undivided. The cells $2a^{1.2}$, $2b^{1.2}$, etc., and $2a^{2.1}$, $2b^{2.1}$, etc., next undergo a laeotropic division, and, at the same time, the three cells of the fourth quartette, $4a$, $4b$, and $4c$, divide in an equatorial direction. Soon afterwards the cleavage of the upper anterior cells of the third quartette, $3b^1$ and $3c^1$, occurs, followed by the division of the cells forming the bases of the arms of the cross ($1a^{1.2}$, $1b^{1.2}$, etc.). The egg now consists of seventy cells,— twenty cells of the first quartette, twenty-four of the second, fourteen of the third, eight of the fourth, and four small cells at the vegetative pole. From this stage on the cells of the third quartette which have not hitherto kept pace with those of the first and second undergo rapid divisions. $3a^{1.1}$, $3a^{1.2}$, $3d^{1.1}$, and $3d^{1.2}$ each give off a small cell toward the ventral pole, and $3b^{2.1}$, $3b^{2.2}$, $3c^{2.1}$ and $3c^{2.2}$ likewise give off a small cell in the same direction at the anterior side of the egg; thus arise four pairs of small cells, two anterior and two posterior. Soon all of the upper cells of the third quartette divide in the same direction as before. There thus results in the anterior

quadrants *b* and *c*, three pairs of cells of the third quartette placed the one above the other, while in the posterior quadrants *a* and *d*, there are three pairs of cells similarly arranged situated above the large cells $3a^2$ and $3d^2$. Before the foregoing divisions of the third quartette are completed the cells $2a^{2.1.1}$, $2b^{2.1.1}$ etc., and $2a^{2.2}$, $2b^{2.2}$, etc., have begun to divide, and there soon follows a cleavage of the four cells at the apical pole ($1a^{1.1}$, $1b^{1.1}$, etc.). Meanwhile the fourth quartette has divided again, making sixteen entomeres in all. With the

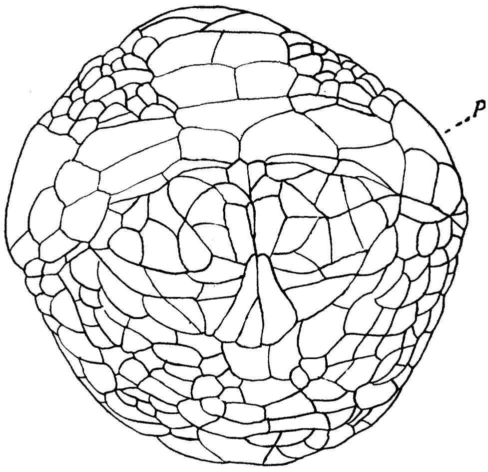

FIG. 3. — Gastrula with the blastopore nearly closed; *P*, prototroch.

cleavage of the basal cells of the arms of the cross the number of blastomeres in the egg reaches one hundred and four. The cells of the third quartette continue to divide quite rapidly, while the cleavage of the second quartette takes place more slowly. The cells of the first quartette whose divisions have hitherto been of the spiral type begin, at the next cleavage, a series of bilateral divisions which result in a longitudinal splitting of the arms of the cross similar to that which was found by Conklin to occur in Crepidula. This splitting first occurs in the anterior arm of the cross; somewhat later the lateral arms begin to divide; the posterior arm, as in Crepidula, remains undivided. The cross develops much more slowly than in the form studied by Conklin. The details of

its history are, in many respects, quite different, and the regularity of its form becomes broken up before it reaches a corresponding degree of development. The cells of the posterior arm enlarge and take part in the formation of the large head vesicle. This enlargement of cells extends to the cells at the center of the cross and finally continues forward to the prototroch; thus the cap of cells lying above the prototroch is cut into two groups of small cells separated by a median band of large, clear cells extending from the head vesicle behind to the prototroch in front. These isolated groups of small cells multiply rapidly and doubtless give rise to the eyes and cerebral ganglia.

The prototroch is formed from the trochoblasts previously mentioned and the uppermost cells of the second quartette which form the tips of the arms of the cross. Possibly other cells of the second quartette may take part in its formation; it is certain that the third quartette has no share in the process. The cells of the prototroch, up to a late stage of development, are few in number, and are arranged in a double row which extends from the ventral side a short distance in front of the blastopore to the head vesicle above. At an early stage they acquire cilia which serve to rotate the embryo in the capsule.

The head vesicle arises mainly from cells of the first quartette lying on the posterior side of the egg. By the enlargement of these cells the apical pole is pushed forward through an arc of 90° so that it comes to lie at the anterior end of the embryo. An apparent effect of this process can be seen in the cells lying in front of the blastopore; many of these cells take on a long, narrow form with their long axes transverse to the median plane of the egg, thus giving the appearance of having been flattened out by pressure from in front.

The cells of the second and third quartettes become so numerous before any organs make their appearance that it is impossible to trace the exact cell lineage of the structures arising from them. All that can be determined is the cell origin of the regions of the body wall from which certain organs are developed. It is quite certain that the cells of the posterior quadrant of the second quartette (derivatives of *2d*)

give rise to the shell gland and the median portion at least of the foot. In fact the cells of the posterior quadrant of the second quartette, with the quadrants *a* and *d* of the third, give rise to the larger part of the body of the embryo.

The cells of the fourth quartette undergo a third division in a more or less equatorial direction and the small cells *A*, *B*, and *C* divide, forming a fifth quartette. The number of entomeres increases still further before gastrulation begins. An embolic gastrula is formed, the blastopore becoming an elongated, slit-like orifice which closes from behind forwards. The lips of the blastopore close for a short time, but the definitive mouth makes its appearance, at a slightly later stage, at the point of closure. Whether or not an actual fusion of the lips of the blastopore occurs cannot at present be stated. The regions in front and behind the blastopore and at the sides are derived from the second quartette, while the cells of the third quartette lie at the angles. In the region around the mouth the cells become large and clear, and this area is continuous posteriorly with a narrow median band of clear cells separating the halves of the fundament of the foot.

The two mesomeres soon after the division of the primary mesoblastic cell come to lie entirely in the cleavage cavity at the posterior side of the egg. Their first division is very unequal and seems to have been overlooked by Rabl. Each mesomere gives off at its anterior end a minute cell, not larger than the first polar body. These cells are clear and lie close together in the cleavage cavity; their further history has not been followed. At the next division of the mesomeres begins the formation of the mesoblastic bands described by Rabl.

Fuller details of the subject of this short sketch will be given in a future paper. It is a source of pleasure to acknowledge the many favors granted me by Prof. C. O. Whitman in connection with this work and the valuable suggestions I have received from Dr. E. G. Conklin.

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